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Vol. 36 No 11

BULLETIN

OF THE

TORREY BOTANICAL CLUB

NOVEMBER, 1909

The development of the sporogonium and adjacent tissues of the gametophore of Conocephalum conicum*

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(WITH PLATES 30–33)

Although several rather extensive articles on the morphology and development of the liverwort *Conocephalum conicum*† have appeared, there are certain interesting and important features of this plant that do not seem, as yet, to have been described. This investigation was undertaken for the purpose of tracing the development of the sporogonium and the surrounding tissue of the gametophore in order to determine the origin of a sheath which surrounds and encloses the calyptra and to see if it bears any relation to the pseudoperianth long known to exist in the related genera *Marchantia* and *Preissia* but said to be lacking in *Conocephalum.* This seemed especially desirable, since the two most recent and important articles ‡ dealing with this plant do not touch upon this interesting structure.

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* *Conocephalum conicum* (L.) Dum. (*Fegatella conica* of most European authors) is one of the larger Marchantiaceae. It is widely distributed in Europe and North America. It grows abundantly in the ravines near Ithaca, N. Y., on moist or dripping rocks. The original post-Linnaean spelling of the generic name appears to be *Conocephalum* Wigg. Prim. Fl. Hol. 82. 1780, though Dumortier and some others have used the form *Conocephalus.*

† Contribution from the Department of Botany, Cornell University, No. 136.

‡ Cavers, F. On the structure and biology of *Fegatella conica.* Ann. Bot. **18**: 87–120. *pl. 6, 7.* 1904.

Bolleter, E. *Fegatella conica* (L.) Corda. Eine morphologisch physiologische Monographie. Beih. Bot. Centralb. 18^1: 327–408. *pl. 12, 13.* 1905.

[The BULLETIN for October, 1909 (36: 557–614. *pl. 26–29*) was issued 30 O 1909.]

The gametophore of *Conocephalum conicum* begins to develop early in June. The archegonia are ready for fertilization about the first of July. The sporogonia develop rather slowly but the spores and elaters are fully formed by the time winter sets in, when growth ceases. At this time the stalk of the gametophore is very short, so that the conical receptacle appears to be sessile on the thallus. During the warm days of the following May, the stalk of the gametophore elongates with some rapidity, lifting the receptacle high above the surface of the thallus. The stalk of the sporogonium itself then elongates, after which the spores are set free by the rupture of the capsule. *

Each archegonium is developed in a flask-shaped cavity or depression on the under side of the archegoniophore. Usually only one archegonium appears in each depression, but rarely two may be found. The archegonium arises from and is attached to the tissue at the base of the cavity in which it is developed, but the neck of the mature archegonium projects through the circular opening of this depression and curves upward toward the lateral margin of the gametophore (*figure 37*). At the time of fertilization the wall of the venter is about two layers of cells in thickness (*figures 1, 6, 37*).

The fertilized egg enlarges until it nearly or quite fills the oblong cavity of the venter (*figure 1*) and becomes enveloped by a deeply staining membrane. The inner surface of the venter is stained intensely (*figures 1, 6, 37*). The nucleus also is stained deeply, its membrane being easily made out, but the cytoplasm is stained diffusely.

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* *Note.* —The first material was put up in May, 1908, when the sporogonia were mature on elongated stalks, and in the beginning of June when there was evidence that the archegoniophores were beginning to develop at the tips of the new thalli. Beginning with July 14, 1908, until August 10, 1908, material collected at Ithaca was carefully packed in moist sphagnum and shipped to New York City where it was kept in a moist vigorously growing condition until it was needed. Collections were made from this material two or three times weekly until September 21, 1908.

All the material used for this work was fixed in chrom-acetic fixing fluid. The gametophores were fixed entire. In all cases care was taken to remove the air from the tissue. For the material put up at Ithaca the large air-pump in the laboratory was used, but for the material fixed elsewhere a small suction pump attachable to a faucet was found as effective as the large air-pump. This treatment of the tissue was necessary for, as is well known, the thalli and gametophores of all the Marchantiaceae contain air which prevents the entrance of fixing fluids as well as other reagents, especially those used in infiltrating and embedding.

All the sections were cut 8–10 μ in thickness, except those of the mature sporogonium containing germinated spores; these were sectioned 5 μ thick. The sections were stained with Delafield's haematoxylin alone or with a counterstain of Bismarck brown.

The nucleus of the fertilized egg soon divides into two, which usually lie close together (*figures 2, 3, 6, 10*), but in some cases they may be separated (*figure 4*). These nuclei are of approximately equal size. They may be parallel or transverse to the long axis of the archegonium. A cell wall is not laid down immediately after the first division of the nucleus but follows tardily.

The first division wall is transverse and is, as are all the walls when newly formed, a delicate membrane. In order to be certain that no walls were overlooked, Bismarck brown, which is well known to be one of the best counterstains for cell walls, was used. This division is followed by two or three successive transverse divisions forming either four or five cells (*figures 7, 8, 9, 11, 13, 16, 17, 32*). As in the case of the first division, the formation of a wall is always subsequent to the division of the nuclei.

In all the material studied, no longitudinal wall was formed until the tier of four or five cells was completed, although about fifty were seen in approximately this stage (*figures 7, 8, 9, 11, 13, 16, 17, 32*). Considerable attention was given to this sequence in the formation of cell walls, since the method observed is at variance with that usually described for this family and especially for this species by Cavers ('04). This author describes the young embryo as divided into octants by one transverse and two longitudinal walls at right angles to each other. My observations accord more nearly with those of Bolleter ('05), but this author describes and figures only four cells formed by three transverse walls.

The outline of the young embryo differs considerably from that of *Preissia* and *Marchantia*, being elongated parallel to the long axis of the archegonium and broader at the distal than at the proximal end (*figures 11, 12, 16*). In the two plants first mentioned it is nearly spherical.

Figure 12 shows the first longitudinal division at the lower or distal end of the young sporogonium; *figure 24* shows a cross section at this stage; *figure 18* a variation, the only one observed.

This first longitudinal wall is soon followed by a second one at right angles to it, so that each one of the original cells is divided into four. These two longitudinal walls are shown in cross section in *figures 14, 23*, and *25*.

While the development just described is progressing in the embryo, periclinal division takes place rapidly in the venter of the archegonium, so that the wall is finally four or five layers of cells in thickness, and the whole structure becomes much more massive (*figures 14* and *16*). Moreover, the tissue forming the original stalk of the archegonium increases, and its cells become rich in protoplasm. Because of their deeply staining contents and their smaller size, there is a strong contrast between them and the adjacent tissue of the gametophore (*figure 37*). The whole calyptra is much thicker and more massive than that of *Marchantia* and *Preissia*.

The young sporogonium next increases decidedly in length (*figures 19, 20, 22, 30*) and the elongating proximal end forces its way into the tissue developed from the stalk of the archegonium, from which it derives its nourishment (*figures 16, 22, 28*). This elongated more slender proximal portion of the sporogonium is the foot or absorbing organ. It is apparent, therefore, that the foot in *Conocephalum conicum* becomes differentiated much earlier in the life history of the sporophyte than in *Marchantia* or *Preissia*. The mature foot is a conical structure deeply imbedded in the tissue of the gametophyte, while in *Marchantia* and *Preissia* it is very short and broad.

The elongation of the embryo is accompanied by repeated transverse division, so that it becomes a clavate structure, many cells in length (*figures 15, 26, 28, 29*). Some of the original transverse walls appear heavy and prominent at this stage (*figures 15, 26, 28, 29*). It seems certain that one of the original four or five transverse walls formed in the embryo separates the capsule primordium from the stalk and foot portion, but whether this is the first original wall cannot be stated positively. *Figure 29* shows a slightly older stage in which one of the original walls is distinct.

Growth is now more rapid in the distal or capsular portion of the sporogonium. By the formation of periclinal and transverse walls it increases in breadth and massiveness (*figures 21, 26, 28,* *29, 31*). During the continued growth of the sporogonium both the foot and capsular portion expand, so that a definite constriction appears (*figures 27, 29, 36*). This constricted portion is the part which later gives rise to the stalk.

In the capsular portion cell division soon gives rise to a single superficial layer of cells which is distinguished from the tissue within, in that its cells are larger and less rich in protoplasm and therefore stain less deeply. This superficial layer becomes the wall of the capsule, while the deeply staining inner tissue, the cells of which have now become arranged in longitudinal rows, is the sporogenous tissue (*figures 27, 36, 39*). At this time the sporogonium fills the cavity of the venter, pressing against its wall.

Certain cells of the alternate rows of the sporogenous tissue become larger than those lying between them, are richer in protoplasm, and have larger nuclei. These are the mother-cells of the spores (*figure 47*). *Figure 53* shows a slightly older stage. These enlarged cells are separated from those surrounding them, become rounded and undergo a period of growth, after which each divides into four tetrahedral spores (*figure 46*).

By the time the tetrads are formed the cells that are to form the elaters have elongated considerably as is shown in *figure 48*, but the characteristic elater-form does not appear until after the spores have become mature in the autumn.

The sporogenous tissue in the capsule of *Conocephalum*, *Preissia*, and *Marchantia* is arranged in longitudinal rows. In the two former plants some of the cells in alternate rows enlarge, separate from the adjacent cells, and become the spore mother-cells, each of which divides into four tetrahedral spores. In the last-named plant, the sporogenous cells divide into groups of four or eight cells each, which always retain their identity as groups, each cell of the group ultimately dividing to form four spores. It has long been known that the spores of *Conocephalum conicum* germinate while still within the capsule (*figure 54*). The spores of *Marchantia* and *Preissia* do not germinate until after they have escaped from the capsule.

During the development of the sporogonium prominent changes take place in the surrounding tissue of the gametophyte, so that at the time of its maturity, it is enclosed not only in the calyptra, but in an additional covering or sheath which lies outside of the calyptra and is derived from the adjacent tissue of the gametophore. This outer sheath does not seem to have been described by any writer on *Conocephalum,* although it was figured in outline by Bolleter (*loc. cit.* 364, *f. A*). This writer makes no reference to this feature, either in the text or in the explanation of his figure. Since no similar organ seems to have been described for any of the other Marchantiaceae, its origin and development will now be considered in detail.

As already pointed out in a previous paragraph, the archegonium of *Conocephalum conicum* is developed in a flask-shaped cavity in the tissue on the under side of the gametophore (*figure 37, 38*). The gametophore of this plant, in common with all other Marchantiaceae, possesses numerous large air-chambers separated by plates of cells. The chambers in the upper part of the gametophore are large and nearly isodiametric. Toward the lateral margin they become smaller and the smallest ones are at the base. The tissue making up the wall of the archegonial cavity on the side toward the stalk of the gametophore is solid at the time of fertilization (*figure 37*), but after this time air-chambers appear in this also (*figure 38*). In the vicinity of the archegonial depression these chambers are long, narrow, and compressed, so that they appear much more slender in longitudinal section than those in the upper part of the gametophore.

At the time of fertilization the archegonial cavity opens to the outside. Through this opening the neck of the archegonium protrudes as has already been stated (*figure 37*). After fertilization the neck of the archegonium withers and turns brown (*figures 34, 38, 40*), as is usual in the bryophytes. Then the lip-cells forming the margin of the opening of the archegonial cavity elongate transversely and grow until those on opposite sides meet and the opening is nearly or quite closed (*figures 40, 44, 45, 52*). As a result of this growth the archegonium with its embryo is contained in a closed cavity.

As the embryo and the calyptra enlarge, the tissue of the gametophore bounding the archegonial cavity on the side adjacent to the stalk of the gametophore elongates rapidly in a vertical direction and since little or no growth takes place on the opposite side the closed mouth of the archegonial cavity is pushed around toward the outside of the gametophore (*figures 40, 45*). Further growth of the sporogonium and calyptra is accompanied by still further development of the tissue separating the air-chambers adjacent to the stalk, so that at maturity the closed opening is found nearly opposite the foot of the sporogonium on the outer side of the gametophore (*figure 44*). The whole outer enveloping sheath is therefore formed by the elongation of the laminae or plates of cells separating the air-chambers in the wall of the archegonial cavity adjacent to the stalk of the gametophore.

At the time the sporogonium has reached the stage of development shown in *figure 45*, and at the time when the spore mother-cells have separated from one another, it may be observed that its growth has not kept pace with that of the calyptra or the enveloping sheath, so that a considerable space appears between the wall of the sporogonium and the surrounding calyptra. The calyptra and sheath, having no support from within, are infolded or collapsed into this depression. As further development takes place the sporogonium comes to fill this space so that the enveloping calyptra and sheath are tightly stretched about the distal end of the sporogonium (*figures 35, 41*).

That the calyptra and sheath do not form one continuous tissue is clearly shown by the fact that the shriveled neck of the old archegonium is found lying between these two envelopes, sometimes closely squeezed between them (*figures 34, 35, 40 41, 50*). That the outer sheath is made up of plates of cells representing the boundaries between air-chambers is clearly shown in *figures 34, 35, 41, 43, 49*, and *51*. An examination of these figures shows that the tissue of the calyptra is composed of cells closely united while the outer sheath is composed, in longitudinal section, of several rows of cells entirely separated from one another (*figures 34, 35, 41*). It should be mentioned that the apparent continuity of the cell walls of the different plates of the sheath, shown in *figures 49, 50*, and *51*, is due to the overlapping of the cells, because the sections are cut in a slightly oblique direction. The true condition is, however, perfectly apparent in *figures 34, 35, 41, 43*, and *45*.

This outer sheath formed from the tissues of the gametophore should not be confused with the pseudoperianth such as appears in certain other Marchantiaceae, *e. g.*, in *Marchantia* and *Preissia*. That structure originates as a collar-like outgrowth from the cells immediately beneath the base of the archegonium, which are descendants from the original cell from which the mother-cell of the archegonium was cut off. Only the slightest indication of this organ appears at the time of fertilization, so that it is an entirely new structure which develops after fertilization has taken place. At its maturity it is a tubular sheath, a single layer of cells in thickness and is never closed or continuous around the distal end of the sporogonium. Such a true pseudoperianth does not exist in *Conocephalum conicum*. It is replaced by the sheath which has already been described as being a further development of the walls of the cavity in which the archegonium is developed. It is composed of several distinct laminae, which are morphologically the plates of cells separating the air-chambers on one side of the archegonial cavity and at maturity completely enclosing the sporogonium and calyptra.

The function of this enveloping sheath may possibly be protective. Since the sporogonium rests over winter in the nearly mature condition, this extra covering, with its air spaces, may serve to prevent excessive radiation and transpiration.

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BIBLIOGRAPHY

Hofmeister, W. On the germination, development, and fructification of the higher cryptogamia. 1862. [English trans.]

Kienitz-Gerloff, F. Vergleichende Untersuchungen über die Entwickelungsgeschichte des Lebermoos-Sporogoniums. Bot. Zeit. **32**: 161–172. *pl. 3, 4.* 1874.

Leitgeb, H. Untersuchungen über die Lebermoose. VI. Die Marchantieen. 1881.

Goebel, K. Outlines of classification and special morphology of plants. 1887. [English trans.]

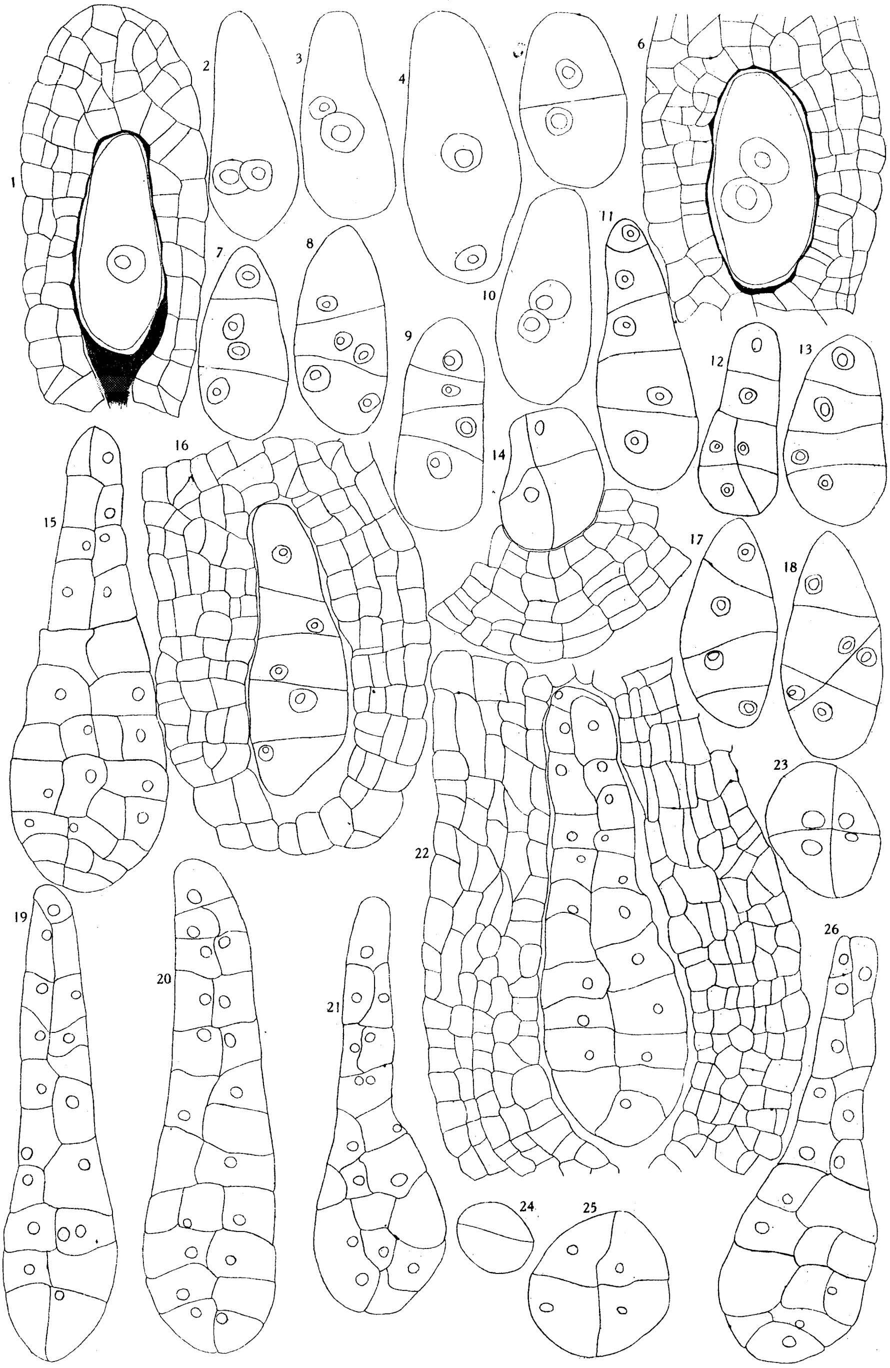
Cavers, F. On the structure and biology of *Fegatella conica*. Ann. Bot. **18**: 87–120. *pl. 6, 7.* 1904.

Bolleter, E. *Fegatella conica* (L.) Corda. Eine morphologisch-physiologische Monographie. Beih. Bot. Centralb. 18^1: 327–408. *pl. 12, 13.* 1905.

Campbell, D. H. The structure and development of mosses and ferns. Second edition, 1905.

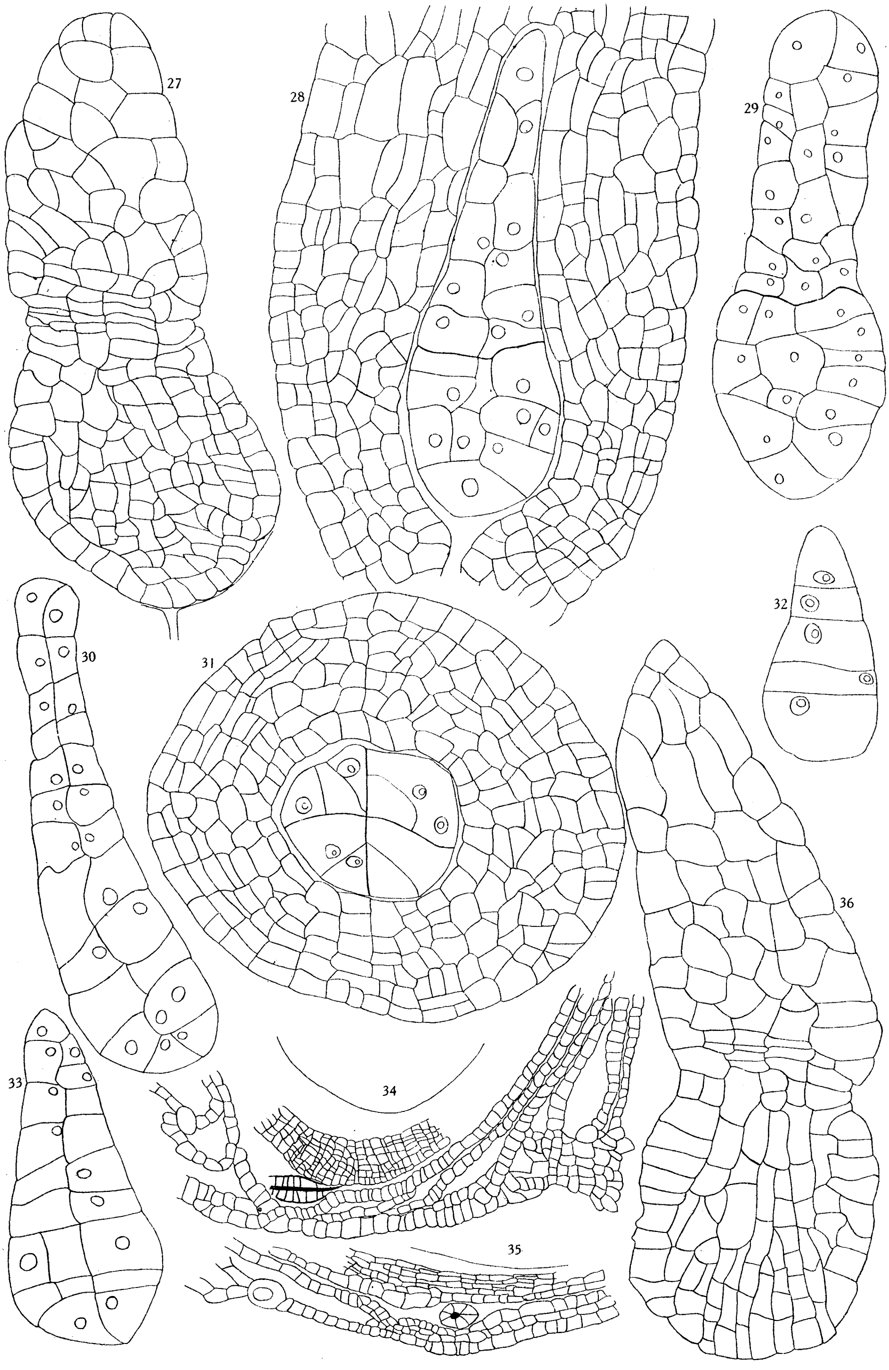
Explanation of plates 30–33

The figures are so freely alluded to in the accompanying text that further explanations would perhaps involve unnecessary repetitions. It should be stated, however, that all the figures were drawn with the aid of a camera lucida. Figures 1–26, 28–33, 46–48, and 51–53 were drawn with a Bausch and Lomb 1/8-inch objective and 1-inch ocular; 27, 36, 37, 39, 42, 49, 50, and 54, with a 1/8-inch objective and 2-inch ocular; 34, 35, 38, 40, 41, and 43, with a 2/3-inch objective and 1/2-inch ocular; and 44 and 45, with a 2/3-inch objective and 1-inch ocular. The original drawings have been reduced one half.



GRAHAM, CONOCEPHALUM CONICUM

COCKAYNE, BOSTON



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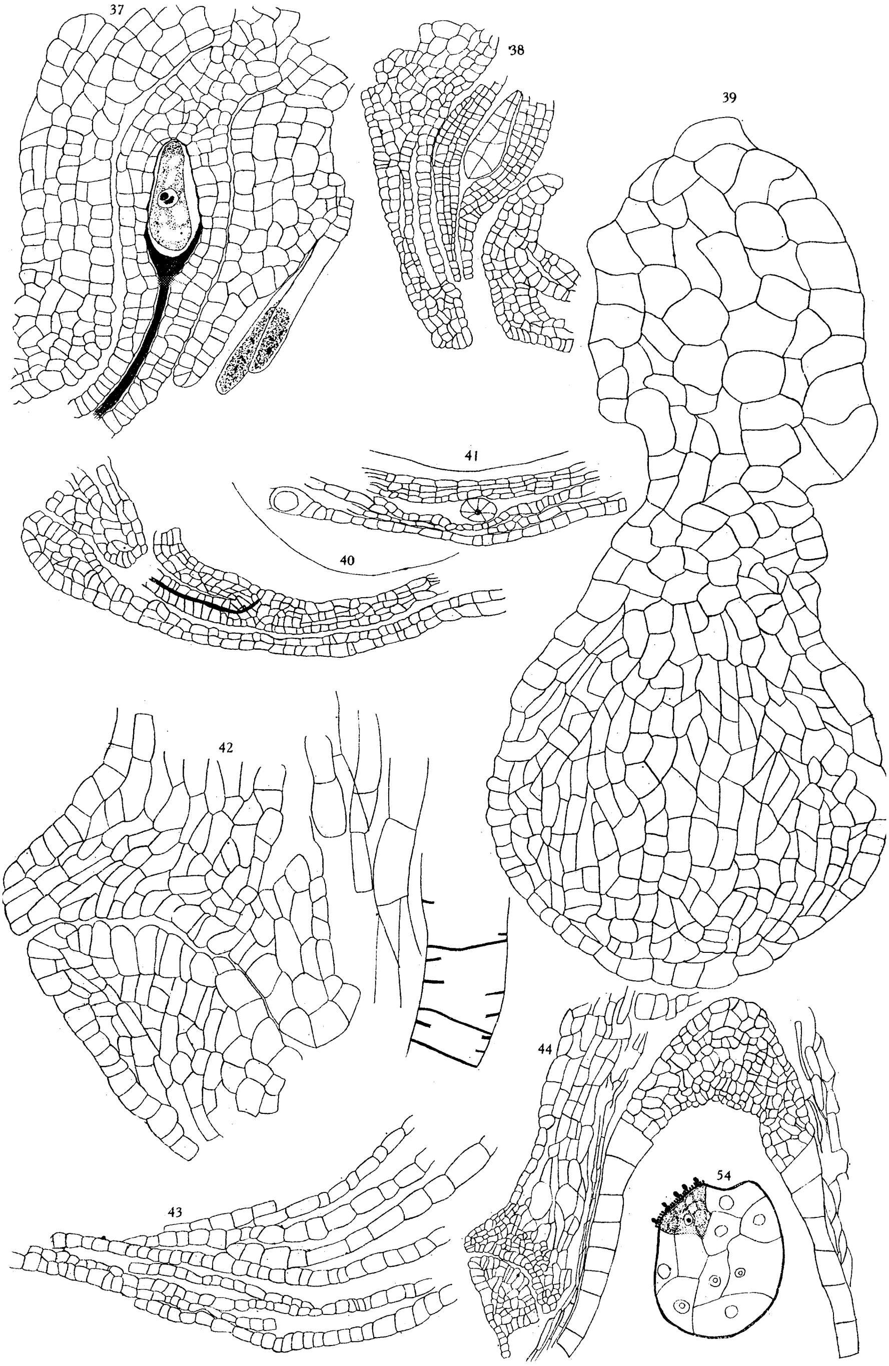
COCKAYNE, BOSTON



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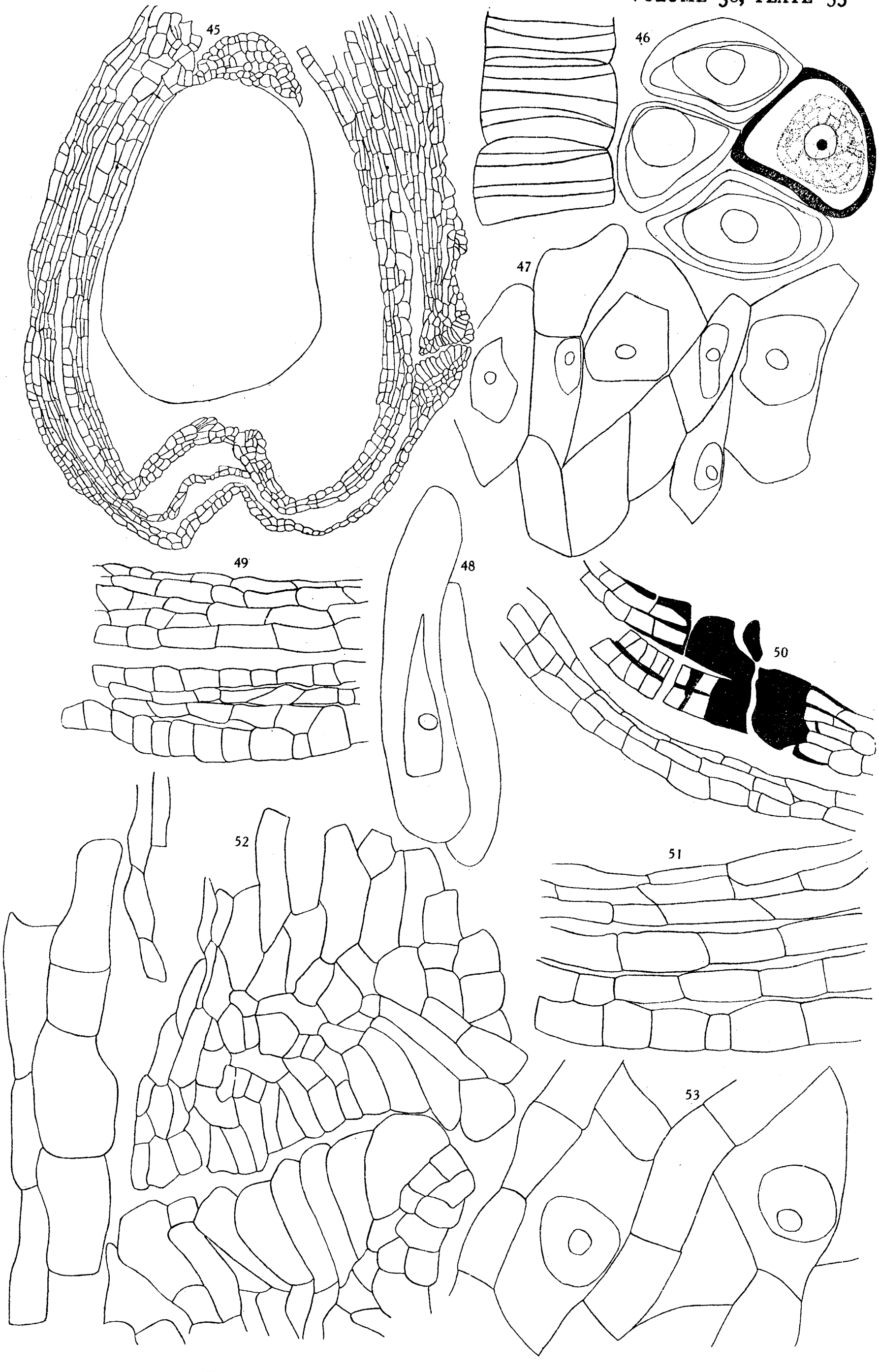

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